

Experimental Induction of Localized Reproduction in a Marine Bryozoan

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Abstract. The control of reproduction and growth rate within colonies of marine invertebrates is often conditional and can be very localized. We demonstrate experimentally large and localized shifts in the timing and pattern of reproduction within colonies of a temperate bryozoan (*Membranipora membranacea*) in response to simulated damage by predators and crowding by conspecifics. In these protandrously hermaphrodite colonies, zooids on the damaged side of a colony reproduced sooner than in unmanipulated regions of the same colony. To examine the influence of the pattern of edge damage on localized reproduction, we damaged the perimeter of circular colonies in two patterns: (1) a continuous half of the edge was trimmed (1/2-Damage) and (2) the edge was trimmed in four alternating one-eighth sections (4/8-Damage). The 1/2-damage treatment triggered localized reproduction, and the more localized four-eighths-damage did not. These experiments demonstrate that the configuration rather than the total amount of edge damage affects the localization of reproduction. In parallel experiments, conspecifics were allowed to crowd half the perimeter of experimental colonies. This treatment also resulted in localized and accelerated reproduction near the contact zone adjacent to a conspecific. Not only do patterns of reproduction change in crowded or damaged colonies, but obstructed colonies also compensate for reduced growth at an obstructed edge by extending the adjacent unobstructed perimeter edge at a greater rate.

One model to explain the sort of local cues governing the observed shifts in reproduction and growth rate is a source-sink model. A similar mechanism is proposed to underly growth and reproductive allocation in plants. We suggest that the balance between growth and onset of reproduction in zooids is determined by the rate of trans-

locate moving through each zooid. The rate of translocate movement through zooids is, in turn, affected by the strength and proximity of sinks for that translocate, such as the growing edge of the colony. We propose a simple source-sink model of carbon flow to explain our experimental results. This model would account for the induction of localized reproduction in 1/2 damaged colonies and the lack of localization in 4/8 damaged colonies.

Introduction

Many organisms do not have fixed life history patterns and are instead plastic in the timing and quantity of metabolites allocated to growth and reproduction (Cohen, 1971; Hickman, 1975; Ryland, 1981; King and Roughgarden, 1982; Schlichting, 1986; Stearns and Koella, 1986; Harvell and Grosberg, 1988; Stearns, 1989). In colonial invertebrates, zooidal responses to biotic and abiotic factors are highly variable because they can be modified, sometimes in a very localized region of a colony, by both intrinsic and extrinsic stimuli (Hughes and Cancino, 1985; Harvell and Grosberg, 1988; Harvell, 1991). In fact, the ability to adjust the shape of modules and the allocation of resources among modules are central characteristics of coloniality (Mackie, 1986; Harvell, 1991). For example, the localized induction of defensive spines or disruption of a growing edge by damage can induce reproduction in a marine bryozoan (Harvell and Grosberg, 1988; Harvell and Padilla, 1990; Harvell, 1991, 1992). In hydrozoan (Cnidaria) colonies, a number of extrinsic stimuli accelerate the onset of reproduction, such as crowding (Loomis and Lenhoff, 1956; Braverman, 1974; Stebbing, 1980) and high carbon dioxide concentration (Crowell, 1957; Braverman, 1974). Despite the ubiquity of resource sharing among modules of colonial invertebrates (Mackie, 1986), there is no theory linking rates or patterns of translocation

there is no theory linking rates or patterns of translocation and resource allocation to growth and reproduction in these organisms.

In other modular organisms such as plants, studies on resource allocation and carbon budgets have revealed the importance of an internal balance of carbon use in determining rates of translocation and subsequent allocation to growth and reproduction (Lang and Thorpe, 1983; Bloom *et al.*, 1985; Chiarello *et al.*, 1989; Chapman *et al.*, 1990; Marshall, 1990). This has led to the development of a source-sink model, which forms the paradigm for carbon (and other metabolite) transport within plants (Chiarello *et al.*, 1989; Marshall, 1990). In bryozoans, translocation of metabolites from central to peripheral zooids has been demonstrated (Best and Thorpe, 1985), but the relationship between translocation patterns and allocation to growth and reproduction remains unknown. Our information on resource allocation within colonies has been largely limited to patterns of reproductive timing rather than experimental investigations of underlying processes.

In this paper, we experimentally investigate how environmental factors such as damage and crowding affect the allocation to reproduction and growth in the marine bryozoan, *Membranipora membranacea*. We examine the applicability of a source-sink model of resource allocation by analyzing how localized disruptions to a growth sink result in localized shifts in the onset of reproduction within colonies. Specifically, we ask how damaging or crowding the colonies' growing edge affects the timing of reproduction of zooids proximal to that edge and how this local disruption affects the growth rate on adjacent undamaged edges. To examine the role that sink strength may play in the observed allocation shifts, we vary the magnitude of damage by cutting different lengths of colony margin in several experiments. Finally, we use our results to develop a source-sink model of rate of carbon flow and resource allocation within a colony to aid in the process of further hypothesis-testing about processes of resource allocation within colonial marine invertebrates.

Materials and Methods

Timing of reproduction

To establish the unmanipulated pattern of onset of reproduction in undamaged and uncrowded colonies, we mapped the distribution of onset of reproduction for zooids within colonies of *Membranipora* through time. Previous attempts to describe the onset of reproduction in colonial invertebrates have proceeded with a descriptive, bulk colony approach (reviewed in Harvell and Grosberg, 1988; but see Dyrinda, 1981; Wahle, 1983, 1984; Brazeau and Lasker, 1990). Colonies of *Membran-*

ipora are sub-annual, protandrous hermaphrodites; each zooid proceeds from non-reproductive to sperm producing to sperm and oocyte producing to only oocyte producing (Harvell and Grosberg, 1988). As reproduction begins within the colony, the number of zooids with gametes and the density of gametes per zooid is low. This is most evident at the onset of oocyte production, because oocytes can be readily counted. Through time, more zooids develop a greater density of gametes. Thus increases in the density of reproductive zooids per colony and oocytes per zooid occur as part of the maturation process. In our experiments, we will equate a greater density of reproductive zooids with a more advanced reproductive state, because there is no indication from previous studies (Harvell and Grosberg, 1988; Harvell, 1992) that our experiments should affect the quantity of gametes produced. To determine whether the timing of reproductive transitions varied within different aged regions of undisturbed colonies, we monitored the reproductive states of zooids from approximately 40-day-old colonies ($n = 11$). From previous studies we knew that 40 days is the approximate age when undisturbed colonies begin producing sperm (Harvell and Grosberg, 1988; Harvell *et al.*, 1990). We could age colonies because we monitored their settlement and growth on lucite panels on which they had naturally settled, which were suspended underneath the Friday Harbor (FHL) breakwater (see Harvell and Grosberg, 1988, for methods). Colonies on these panel were sampled at three, approximately eight-day intervals in mid July 1987.

The lucite substrates were easily manipulated and could be brought from their storage locations in the field to the lab for monitoring. Panels were maintained in a running seawater system for the 2–5 h they were in the lab, and during the approximately 20 min sampling were kept submerged in cool water under the dissecting microscope. Reproductive states were monitored under 12 \times with a Wild dissecting microscope and fiber optic lights. Within-colony variation in reproductive state was measured by determining the reproductive state of five haphazardly chosen zooids within each of three regions of the colony. Depending upon the size of a colony, each of these regions might be populated by greater than a hundred zooids. Nonetheless, the variance in reproductive state among the five sampled zooids was low. The sampling was truly haphazard because the reproductive state of a zooid could not be determined prior to scrutinizing with a dissecting microscope and zooids were sampled from all parts of the particular region. The configuration of regions sampled from each approximately circular colony was three concentric bands of equal diameter, but decreasing age: ancestrula region (A) (the founding, morphologically distinct "twinning" zooid is at the approximate center of the colony

and is called an ancestrula), mid region (M), and edge or new growth region (E) (Fig. 1). The width of these regions was determined by counting the total number of rows containing developed zooids in the colony and dividing by three. Reproductive states were easily assigned because both sperm and oocytes were visible under microscopic magnification through the transparent frontal membrane of the zooids. Each zooid was assigned a numerical value for its reproductive state from 0 to 4, and the median of the five values was analyzed in subsequent statistical analyses. A colony was classified as non-reproductive if the median state was 0 or 1 and as reproductive if those measures equalled or exceeded 2. Stage 2 was an unambiguous indicator of active reproduction because the sperm are actively moving and refract light, showing bright birefringence.

- 0 = non-reproductive
- 1 = sperm morulae present and visible on the underside of the frontal membrane
- 2 = mature spermatozeugmata present (bundles of actively moving and light refractive sperm)
- 3 = oocytes present (and sperm also)
- 4 = only oocytes present.

Partial damage experiments

New zooids are produced at the outer periphery of a colony and develop from buds to feeding zooids over several days. Colonies of *Membranipora* are indeterminate growers and continue to expand at the periphery by producing new buds until the colonies begin to senesce in late summer (Harvell and Grosberg, 1988; Harvell *et al.*, 1990). Although we had previously shown that damage to the margin of a colony accelerates the sexual development of the zooids proximal to the margin (Harvell and Grosberg, 1988), the degree of localization of this effect was unknown and we did not consider how subsequent growth of zooids would be affected by damage. Could the onset of reproduction be accelerated in one part of the colony in response to localized cues and remain unaffected in another part of the colony? It also appeared that growth of a colony was accelerated on a side away from damage, so we also tested the hypothesis that compensatory growth occurred in response to damage.

Working with single colonies naturally settled to lucite panels, we trimmed the outer edge buds back approximately one millimeter (equivalent of one zooid row) with a razor along half the perimeter of 14 colonies and monitored them from 13 to 24 July 1987 (1/2 damage treatment). We monitored 13 other undamaged colonies as controls. At two-day intervals, we determined the reproductive state of five zooids from three regions (A, M, E) on both the damaged and undamaged half of a colony.

Colony areas were determined from tracings of the colonies made at 2-day intervals during the 11-day duration of the study. To test the hypothesis that compensatory growth occurred on the undamaged side of the colony in response to damage, the linear rate of growth was measured on controls and damaged colonies as the distance from the ancestrula to each opposite edge and the areal growth as the total area added to colonies. These were analyzed with linear regression of area and growth distance against original colony size. A linear model was used because both the control and damaged colony data fit this model well over the range for which we have data.

To determine how localized the stimuli triggering reproduction could be, we also divided 15 moderate-size (approximately 2000 mm²) colonies into eighths and damaged alternating one-eighth lengths of the perimeter (4/8-damage treatment; see Fig. 4 below) and monitored growth and reproduction of the zooids proximal to damaged and undamaged regions. This set of experiments was performed on equal-sized, uncrowded colonies growing naturally on kelp blades and returned to lines off the breakwater after trimming. The colonies were sampled once, 16 days after trimming. For experimental colonies, reproductive states were recorded for five zooids 2–4 mm proximal to each of the four damaged and four undamaged sections of the colony edge. Eight corresponding regions were sampled on undamaged control colonies from the same kelp blades.

Effects of crowding by conspecifics

Harvell and Grosberg (1988) showed that the onset of reproduction was accelerated in colonies that were completely surrounded by conspecifics. In the current study, we designed experiments where colonies were only crowded on one side with a single conspecific to assess whether the crowding-induced reproduction was localized like the response to damage. We investigated both the influence of size and partial crowding on timing of reproduction. We grew 23 pairs of unequally sized (and aged) colonies on lucite panels. This size asymmetry was engineered by removing all colonies settled on the plate except those of particular sizes and distances apart. The size asymmetry was of no particular importance to this study, but it was important for data taken from the same experiment and reported in Harvell and Padilla (1990). At the start of the experiment, the small colony of each pair was an average size of 500 mm² and the large colony was an average size of 2500 mm². Because growth stops along the common border after contact, we designated zones to sample as in the 1/2-damage treatment. Colonies were sampled on alternate days for 13 days following contact. Data were pooled into three intervals: <8 days, 8–9, and

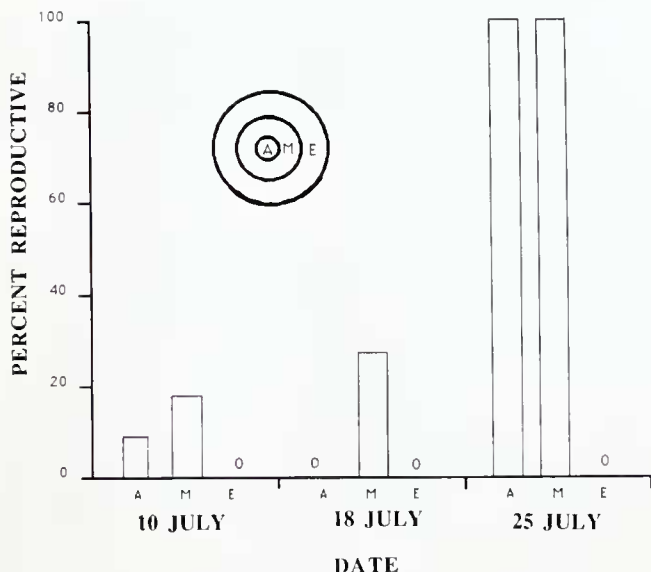


Figure 1. Percentage of control colonies producing spermatocytes or oocytes at three dates. Median percentages were calculated from five zooids haphazardly sampled from each of three regions in 11 colonies (A, M, E = Ancestral, Mid, and Edge regions). Both within-colony location ($\chi^2 = 10.49$, $P = 0.005$) and date ($\chi^2 = 7.91$, $P = 0.02$) significantly affect the frequency of reproductive colonies.

10–13 days after contact. Five zooids were again sampled from each region, and the median of those values analyzed. Because the shapes of colonies became so distorted in the crowding treatment due to compensatory growth away from the interaction, it was impossible to consistently sample the same three regions as on the controls (A, M, E). We therefore divided the crowded colonies into regions of two (M, E) instead of three equal radii for sampling.

Results

Timing of reproduction

Under normal, good-growth, field conditions, colonies begin reproduction as males at an age of approximately 40–60 days and would be approximately 2500 mm² in area (Harvell, 1992). The pattern of reproduction in unmanipulated colonies is for older zooids near the ancestrula and in the mid regions of colonies to reproduce first (Fig. 1). Most zooids are producing spermatocytes and oocytes by late July.

The significant results of the log-linear test reflect the transition in ancestral and mid regions of colonies from a non-reproductive to reproductive state between 18 and 25 July (Fig. 1). By 25 July, the percentage of ancestral and mid-colony regions that are reproductive has increased from 0 to 25%, respectively, to 100%. These data

do not allow us to differentiate timing of reproductive events in ancestral and mid-colony regions because both regions became equally reproductive; zooids from the edge were still not reproductive (Fig. 1).

Partial damage experiments

In the 1/2-damage experiment, the damaged side produced both sperm and eggs sooner than the non-damaged side (Fig. 2). Reproduction began on the damaged side approximately 5–6 days after trimming (Fig. 2). Unlike control colonies and undamaged sides of the experimental colonies, reproduction was greater at the edge relative to the ancestral regions on damaged halves. This pattern is also evident 8–9 days after trimming: more colonies are reproducing on the damaged side and more colonies are reproducing at the edge than nearer the ancestrula.

Eight to nine days after damage (18 July) the effects of location within the colony are significant, but the effects of proximity to damage are not (Fig. 2). The location effect is a result of the mid and perhaps edge regions beginning to reproduce, but the center not (Fig. 2).

Three days later (11–12 days after damage) the effects of proximity to damage are pronounced (Fig. 2). The within-colony location term is no longer significant, although inspection of Figure 2 does reveal a tendency for reproduction to vary with location within the colony.

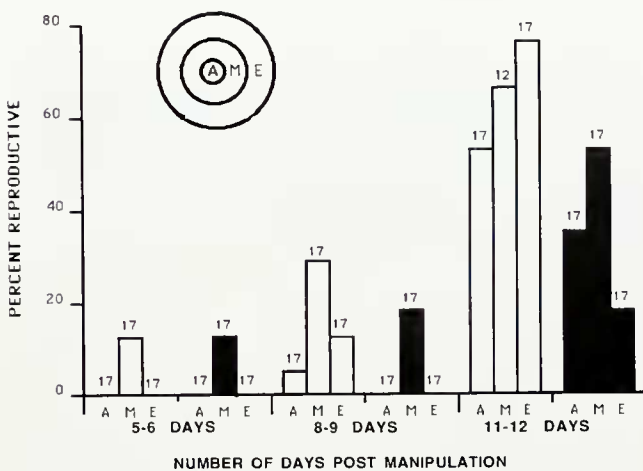
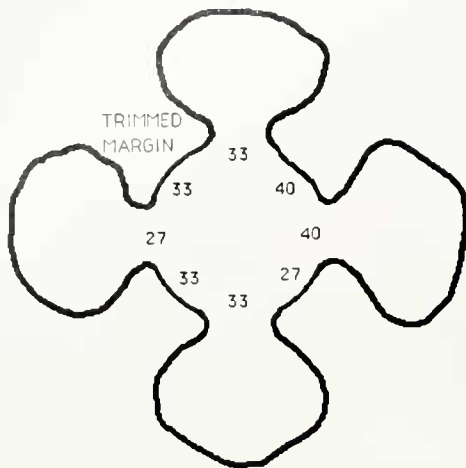


Figure 2. 1/2-damage Experiment: median percentage of colonies producing oocytes or spermatocytes. Reproductive states were tabulated for damaged (open bars) and undamaged (shaded bars) halves of colonies and three regions within each colony (A, M, E). Sample size at top of each bar. At 5–6 days the frequency of reproductive colonies is identical for damaged and control colonies. At 8–9 days, within-colony location affects the frequency of reproductive colonies ($\chi^2 = 7.12$, $P < 0.03$) but proximity to damage does not ($\chi^2 = 2.59$, $P = 0.11$). At 11–12 days, proximity to damage affects the frequency of reproductive colonies ($\chi^2 = 9.05$, $P = 0.003$), but within colony location does not ($\chi^2 = 2.22$, $P = 0.33$).

4/8- DAMAGE TREATMENT



UNDAMAGED CONTROL

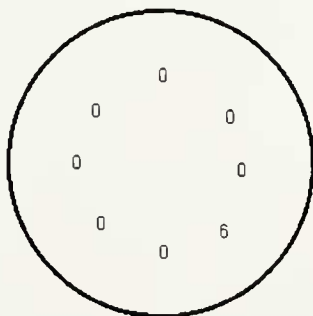


Figure 3. 4/8-damage Experiment: median percentage of colony regions producing oocytes or spermatocytes in 4/8-trim and control colonies 16 days after damage. Numbers are the median percentage of colonies producing spermatocytes or oocytes. The frequency of reproductive colonies varies in 4/8 damaged colonies relative to control colonies ($\chi^2 = 28.41, P = 0.00$); proximity to damage does not significantly affect reproductive timing ($\chi^2 = 0.03, P = 0.86$).

Proximity to damage is clearly a strong effect, the median percent of reproductive colonies is double adjacent to the damaged edge in comparison to the undamaged sides of the colony (Fig. 2).

The pattern of reproduction in the 4/8-damaged colonies was different from the 1/2-damaged colonies. All the colonies were sampled 16 days after the edge was trimmed. Although a higher proportion of trimmed colonies than untrimmed were reproductive, there was no regionalization of reproduction within the damaged colonies (Fig. 3). Our expectation was that, like the 1/2-damaged colonies, reproduction would be localized and proximal to the trimmed edges. Instead, reproduction was uniformly accelerated in all zooids sampled, irrespective of their proximity to the damaged edge. The log-linear

test comparing the 4/8-damage and their controls detected no significant differences in the within colony variation, but a highly significant treatment effect, confirming a generalized increase in reproductive activity in the 4/8 damage colonies (Fig. 3).

Effects of crowding by conspecifics

In paired colonies sharing a crowded edge, the response of colonies was analogous to the 1/2-damage experiment. Zooids on the obstructed side of a colony showed a higher median percent reproduction than zooids from the unobstructed side of the colony at 8–9 days (Fig. 4). For colonies in contact for less than eight days, there were no significant differences in reproduction (Fig. 4). At 8–9 days, colonies crowded with a single conspecific began to reproduce locally near the contact point. In the log-linear test of frequencies at 8–9 days, the within colony location and the proximity terms were significant (Fig. 4).

The pattern was different at 10–13 days after contact. The frequency of reproduction was still higher on the contact side than the non-contact side. The within colony localization term was clearly significant, with the edge region in both treatments showing the highest reproduction (Fig. 4).

Compensatory growth

Patterns and rates of growth on untrimmed halves of colonies were also affected by the manipulation. We

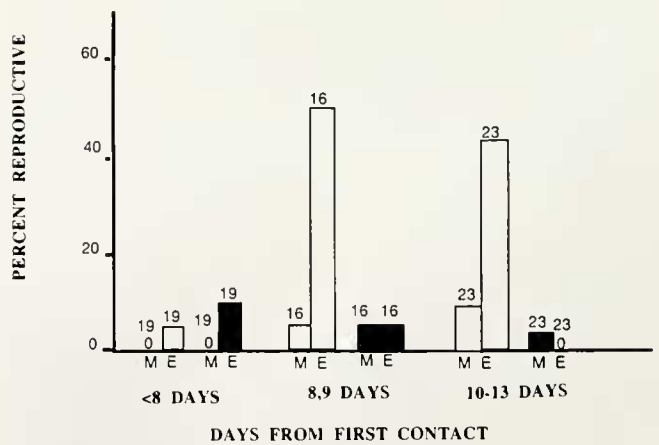
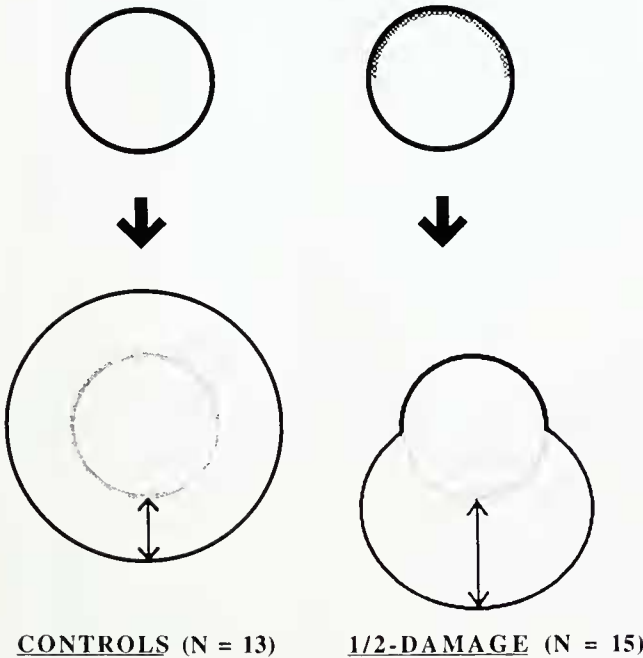


Figure 4. Crowding Experiment: median percentage of colonies producing oocytes or spermatocytes on obstructed and unobstructed sides. Open bars are obstructed sides, closed bars are unobstructed sides of colonies. Sample size at top of each bar. At <8 days post contact, neither location within colony ($\chi^2 = 0.00, P = 0.95$) nor proximity to conspecifics ($\chi^2 = 0.35, P = 0.55$) affected frequency of reproductive colonies. At 8, 9 days post contact, both location within colony ($\chi^2 = 4.99, P = 0.02$) and proximity to conspecific ($\chi^2 = 4.99, P = 0.02$) significantly affected the frequency of reproductive colonies. At 10–13 days post contact, both location within colony ($\chi^2 = 4.49, P = 0.03$) and proximity to conspecifics ($\chi^2 = 7.14, P = 0.007$) significantly affected the frequency of reproductive colonies.

COMPENSATORY GROWTH



CONTROLS (N = 13)

1/2-DAMAGE (N = 15)

Figure 5. Diagrammatic depiction of the appearance of compensatory growth in the 1/2-damage treatment. The shaded area on the initial half-damage colonies indicates where the edge was trimmed. The compensatory growth of the half-damaged colonies was detected as a greater edge extension rate relative to an undamaged control colony.

monitored growth in the damage experiments and found that colonies responded to localized damage by directed, compensatory growth. Figure 5 shows a representation of compensatory growth defined as an increased area-specific edge extension rate. The increase in edge extension was detected on the undamaged side of 1/2-damaged colonies relative to control colonies (Fig. 6a). When growth was disrupted by trimming on one side, intact sides of the colony responded with an elevated edge extension rate. The size-specific rate of extension of a normal colony was less than the rate of extension of the untrimmed half of an experimental colony, as indicated by the difference in intercepts of the regressions of edge extension on initial area (Fig. 6a). This indicates that the undamaged edge was growing faster on damaged than on undamaged colonies. The analysis of covariance [ANCOVA] revealed a significant effect of the covariate (initial area) in the model and no significant difference in the slopes (included in the initial area*damage term) (Table 1a). The damage treatment significantly affected the intercept when the insignificant slope term was dropped from the model. Thus irrespective of colony size, the rate of edge extension is greater for previously damaged than control, undamaged colonies.

We also compared the area added to the 1/2-damage and control colonies over the same time interval. The total area added to damaged colonies was less than that added to undamaged colonies, as indicated by differences in slope of the initial area against area added plot (Fig. 6b). The ANCOVA showed significant effects of the covariate and slope differences between the two treatments (Table 1b). There was no effect of damage on the intercept in the area analysis. Colonies thus responded to trimming by not only accelerating the onset of reproduction in the damaged half, but also by accelerating growth in a direction away from the damage.

Discussion

Despite a widespread recognition that the population dynamics and biology of modular organisms differ from those of unitary organisms, on which most ecological theory is based (Harper, 1981; Jackson *et al.*, 1985; Harper *et al.*, 1986), many fundamental aspects of their biology are little studied. These aspects include the physiological integration of colonial invertebrates, the nature of the interaction between zooid and colony level processes, and particularly inter-zooid allocation phenomena. Wahle

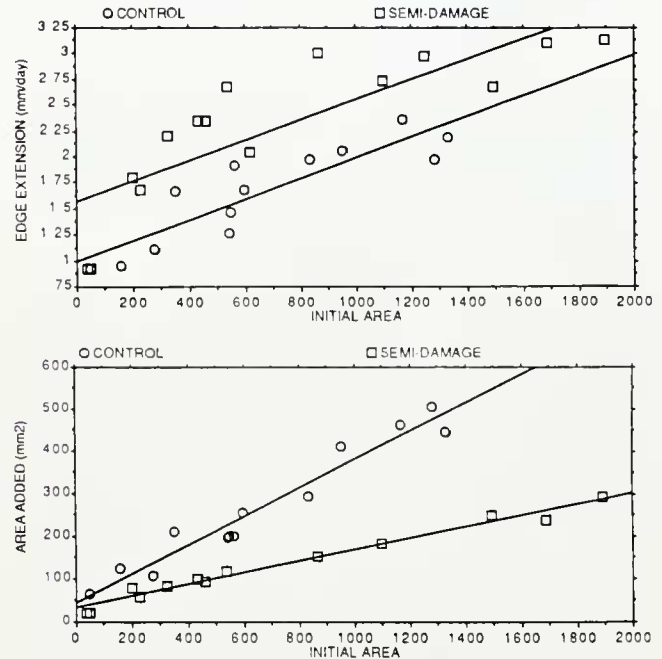


Figure 6. (Top) Compensatory growth measured as an increase in the linear extension rate in 1/2-damaged colonies. Linear regression for control colonies is $Y = 0.0001X + 0.991$ ($r^2 = .783$) and for experimental colonies is $Y = 0.00098X + 1.566$ ($r^2 = .691$). (Bottom) Compensatory growth measured as area added to 1/2-damaged and undamaged colonies. Linear equation for control colonies is $Y = 0.336X + 44.289$ ($r^2 = .972$) and for experimental colonies is $Y = 0.135X + 33.089$ ($r^2 = .978$).

Table I

Analysis of covariance [ANCOVA] on compensatory growth

SOURCE	DF	TYPE III SS	MS	F	P
EDGE EXTENSION					
INITAREA	1	5.110	5.110	34.97	0.000
DAMAGE	1	0.352	0.352	2.41	0.133
INITAREA*DAMAGE	1	0.075	0.075	0.52	0.478
INITAREA	1	6.389	6.389	44.58	0.000
DAMAGE	1	1.819	1.819	12.69	0.001
AREA ADDED					
INITAREA	1	326748.148	326748.148	449.62	0.000
DAMAGE	1	273.040	273.040	0.38	0.546
INITAREA*DAMAGE	1	59380.424	59380.424	81.71	0.000

The first ANCOVA result is for the data plotted in Figure 5a, the edge extension rate by colony size for damaged and undamaged colonies. Because the slope was not significantly different, the interaction term [INITAREA*DAMAGE] was deleted from the model. In the second run of the edge extension analysis, the effects of damage on the intercept are significant. The second ANCOVA result is for the data plotted in Figure 6b, the daily area added by colony size for damaged and control colonies.

(1983, 1984) showed experimentally that rates of regeneration vary in different regions within colonies of tropical gorgonians and that timing of reproduction is dependent upon colony size. Similarly, Brazeau and Lasker (1990) found gradients in the distribution of reproductive function within gorgonian colonies. Physiological and reproductive gradients have also been reported from colonies of bryozoans (Dyrynda, 1981; Harvell, 1984). However, none of these studies attempted to explain processes underlying the observed patterns. We have therefore taken the logical step of experimentally manipulating colonies to examine hypotheses about these underlying allocation processes.

Coloniality and self-regulating processes

The modular, often hierarchical, construction of colonial invertebrates permits varying degrees of integration and autonomy among the component zooids. This type of organization allows the operation of self-regulating processes among the zooids within colonies, adjusted in response to local physiological cues (Harvell, 1991). Because many colonies are large relative to the spatial grain of their environment (*e.g.*, a single colony can simultaneously experience multiple environments), the use of local cues permits partitioning of function within a colony in response to environmental variation. In plants, the flow of resources from sources to sinks provides a mechanism by which local processes such as variation in growth rate or disruption of a metabolite sink can govern the timing and location of growth and reproduction (Watson and Caspar, 1984; Marshall, 1990). In *Membranipora*, a disruption of the colony growing edge appears to accelerate the onset of reproduction in zooids proximal to that edge.

We suggest that the mechanisms underlying this transition are based on a change in the strength of the sink at the distal edge of the colony. Normally, the edge, which has no actively feeding zooids and so must be subsidized by translocated metabolites from more proximal zooids, functions as a sink. Each feeding zooid must acquire carbon both for its own maintenance and for colony maintenance tasks such as growth of the margin or regeneration of lost zooids. We hypothesize that zooids reproduce proximal to a disrupted sink because they are now able to directly use more of the share of carbon normally translocated to the edge of the colony. When net carbon input to a zooid exceeds that required for maintenance, the zooid becomes reproductive. This is a simple self-organizing principle that could explain the observation of localized reproduction proximal to disrupted growth sinks within a colony.

Colony architecture and the source-sink model

In bryozoans, metabolites are transported through the funicular system, a strand of nutritive and nervous tissues that joins successive zooids in the colony (Bobin, 1977; Lutaud, 1977; Best and Thorpe, 1985). The funicular system connects adjoining zooids through pore-plate cellular junctions between the zooids. The special cells in the pore plates are morphologically polarized, suggesting that lipids are preferentially transported from proximal to distal (Bobin, 1977). Each *Membranipora* zooid is pierced by 12 communication pores, so that it is connected with each of the six zooids surrounding it. Little is known about the directions and rates of nutrient translocation in cheilostome bryozoans, but transport from central regions of the colony to the edge has been confirmed with radioisotope

tracer studies (Best and Thorpe, 1985; Miles, Harvell, Griggs, and Eisner, unpub.). Furthermore, even colonies fed near the growing edge only translocate to the nearest edge, confirming that transport is unidirectional (Miles, Harvell, Griggs, and Eisner, unpub.).

The simplest model of translocation assumes equal transport through all pores of a zooid, with rates determined by sink strength. Because axial pore plates are slightly different than lateral plates morphologically, it is not unreasonable to hypothesize higher transport axially than laterally. Both because of a bias to axial transport and because the growing margin of a colony is a strong carbon sink, transport rates should be greatest in a distal direction. In Figure 7 a hypothetical model of the direction and quantity of carbon flow through zooids for each of the sink disruption treatments is shown. Although transport is normally polarized in a proximo-distal direction, this polarity can presumably be reversed to support re-growth in proximal regions of the colony when these are damaged (Jackson and Palumbi, 1979; Harvell, 1984). When the edge sink is disrupted, the polarity of translocation should change and the flow of carbon either be redirected to the next most active sink or zooids at the edge should reproduce with the surplus carbon. In the case of the 1/2-damage treatment, the next sink is on the other side of the colony and so the response might be reverse translocation. Because the sink is so distant, the translocation is expected to be weak and zooids keep most of the carbon they take in (Fig. 7B). In the case of the 4/8-damage treatment, the next sink is adjacent to the short length of disrupted edge and is still in close proximity to zooids via the lateral pores (Fig. 7C). Thus we hypothesize that the zooids in the 4/8-damage experiment remained nonreproductive because active sinks close by continued to use metabolites. Such a mechanism would produce the results we observed: (1) the onset of reproduction in parts of the half-damage colonies, (2) the lack of regionalization in the 4/8-damage experiment, and (3) the compensatory growth observed in the 1/2-damage experiment. Although colonies in the 4/8-damage treatment showed no regionalization in timing reproduction, there was a slight increase in reproduction throughout the colony relative to the controls. This is consistent with our model; removing half the perimeter slowed down diffusion of metabolites throughout the entire colony, but no region was far enough from a sink to show localization.

We have demonstrated not only localized accelerations of reproduction within colonies, but also an associated and localized acceleration in edge extension rate in non-damaged regions of trimmed colonies. To our knowledge, such compensatory growth (an increased area-specific edge extension rate) has not been shown previously for colonial invertebrates. In this case, the increased edge extension

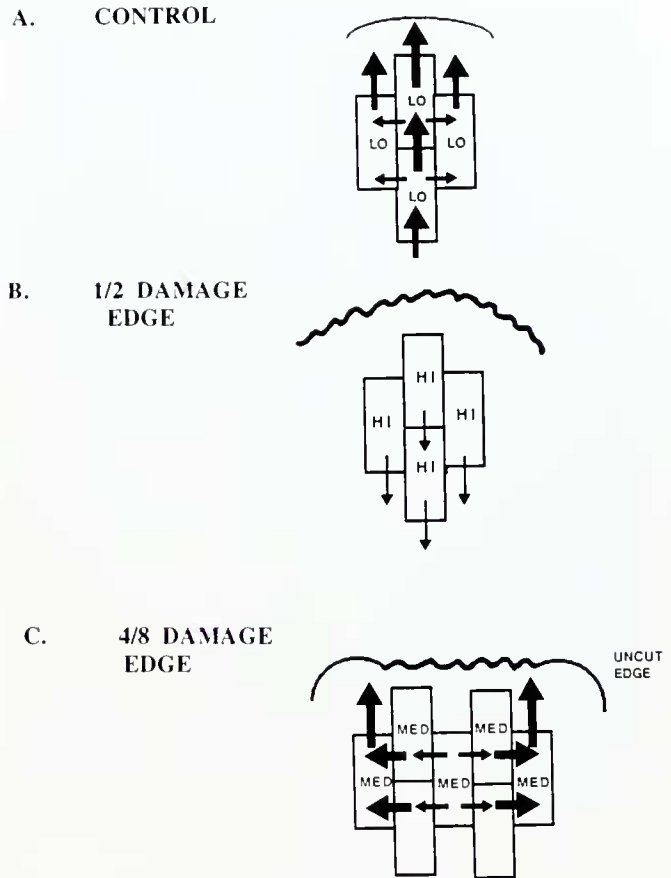


Figure 7. The source-sink model of carbon allocation in cheilostome bryozoans. The hypothesized allocation of translocate is depicted for the three experimental treatments described in this paper. A: Control, B: 1/2-damage (one half the perimeter of a colony removed in a continuous section), C: 4/8-damage (one half the perimeter of a colony removed in four alternating sections separated by four sections of undamaged perimeter). The thickness of the arrows is proportional to the quantity of carbon transported across zooidal boundaries. The labels, Lo, Med, Hi designate the relative amount of translocate retained by a zooid. Thus for control colonies, only a low proportion of the carbon is retained by a zooid. In contrast, when the sink is disrupted as in the half-damage treatment, and there is no close replacement sink, the carbon is not translocated and zooids retain a high proportion. The higher proportion of retained carbon could be used to grow gametes, thus accounting for localized reproduction in zooids adjacent to disrupted sinks. In the 4/8-damage, the original sink is disrupted but an adjacent sink still strongly affects zooid translocation.

rate was not sufficient to allow the damaged colonies to add the same area as the undamaged colonies of the same size. A localized increase in edge extension adjacent to an obstructed edge once again suggests an extremely plastic, colony-wide source-sink allocation budget. We hypothesize the following mechanism to account for the shift. Because the edge of the colony is normally subsidized by proximal zooids and thus represents a sink for metab-

olites, removing the edge disrupts the flow of metabolites. Some of the carbon is used locally by zooids for reproduction and some of the carbon is redirected to the nearest sink—the undamaged edge. In this situation, the undamaged edge adjacent to damage can grow more rapidly, because it is supplemented by more zooids than normal. This also suggests that normal colony growth rates are limited by metabolite availability and that if more internal zooids could be added to subsidize the edge then the colony would extend across the substrate at a greater rate.

An important consequence of modularity may be the ability to continually re-allocate the priority of resource transport among the units of a colony as the environment changes. The existence of thresholds within zooids that determine major shifts in physiology from growth to reproduction, permit zooid specialization, depending upon their location within the colony. The nutrient flow patterns we have proposed remain hypothetical, but are testable using radioisotopes to trace the fate of newly acquired carbon (Best and Thorpe, 1985; Miles, Harvell, Griggs and Eisner, unpub.). We propose that these allocation capabilities are general for cheilostome bryozoans and, in some form, for all colonial invertebrates. Further experimental work is needed to test models of energy flow through colonies in relation to taxonomic identity and levels of physiological integration.

Acknowledgments

This work was supported by NSF OCE-8796230 and OCE-8817498. Assistance with the field sampling was provided by D. K. Padilla, with data analysis by C. Griggs, and with statistical analysis by M. Geber. The manuscript was improved by comments from D. Shapiro, M. Geber, M. Bertness.

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